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CORAL REEF RECOVERY ON GUAM (MICRONESIA) AFTER CATASTROPHIC PREDATION BY *ACANTHASTER PLANCI*¹

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Abstract. At Tanguisson Reef, Guam, in 1968–1969 a population explosion of the coral-eating sea star *Acanthaster planci* devastated the coral community. In the wake of this predation, coral species richness, density, and cover were drastically reduced, and the species composition was altered. In two of three reef zones examined, <1% coral cover remained. At the time of disturbance, some considered the magnitude of this and similar *Acanthaster* disturbances unprecedented, and predicted long recovery times because reefs were viewed as mature, stable communities. This major disturbance offered an opportunity to study the processes and rate of community recovery. Using the data from previous studies in 1970, 1971, and 1974, and my data from 1980–1981, I present a long-term analysis of coral community development. I have focused on coral recruitment, survivorship, and species settlement patterns in relationship to the remnant surviving population.

The preference of *Acanthaster planci* for certain prey (e.g., *Montipora* and *Acropora*) shifted the species composition to one in which nonpreferred prey predominated (e.g., *Porites* and *Leptastrea*). The predominance of nonpreferred prey was short-lived, and by 1980, preferred prey were the primary colonists of two zones. The three biological zones (reef front, submarine terrace, and seaward slope) had their own characteristic species assemblages soon after the disturbance. Nonrandom recruitment or survival of juvenile corals (diameter ≤ 4 cm) established these zones. Although the percentage of juvenile corals fell throughout the survey, their highest density was reached after adult colonies were established. In 1980, of the 34 species examined, 79% showed a significant coefficient of association between adult and juvenile conspecifics. This association caused clumped species dispersion patterns to develop within zones. As the result of recruitment, species diversity rose from 84 species in 1970 to 154 species in 1981. As surviving corals and new recruits developed, the distribution of coral growth forms became more diversified. There was a drastic increase in coral cover (e.g., submarine terrace zone, 0.9% in 1970 to 65% in 1981). This increase in cover corresponded to an increase in size and number of the coral colonies.

In 12 yr, species richness, cover, and composition reached or exceeded measurements of comparable reefs before the disturbance. The recovery occurred faster than predicted by a stable equilibrium model because long-term successional changes were not required. Recovery was accelerated because *Acanthaster* did not destroy the structural integrity of reef framework. This rapid recovery from a natural disturbance demonstrates that some coral communities have a greater resilience than was once believed.

Key words: *Acanthaster planci*; compensatory mortality; contagious distribution; coral reef; disturbance; Guam; nonequilibrium; predation; recovery; recruitment; zonation.

INTRODUCTION

Throughout the Indo-Pacific, in the late 1960's, population outbreaks of the coral-eating starfish *Acanthaster planci* Linnaeus seemingly threatened the reef ecosystem (Chesher 1969a, b, Endean 1973, 1974, Potts 1980, Pearson 1981). In the coral reef, then generally assumed to be the epitome of a mature, stable community, populations were not supposed to fluctuate greatly. Coral reefs were viewed as highly organized, stable ecosystems with their populations in equilibrium (Odum and Odum 1955, Margalef 1968, Grassle 1973). Major disturbances, such as the outbreak of *Acanthaster*, were considered rare, and because of the

reef's supposed great ecologic maturity, recovery was thought to require a long successional process (Endean 1973, 1974, 1977). Disturbances were expected to be long felt within the community (Ricklefs 1973:767). Many workers believed that the magnitude of the damage caused by *A. planci* was unprecedented, and it was predicted that recovery would take many decades (Goreau et al. 1972, Endean 1973, 1974, Endean and Stabulum 1975). Even the possibility of extinction of the scleractinian order was raised (Chesher 1969a). This major disturbance offered an opportunity to study processes involved in coral reef recovery and the rate of the recovery. In this example of coral community development, I have focused on coral recruitment, survivorship, and species settlement patterns in relation to the remnant parent population.

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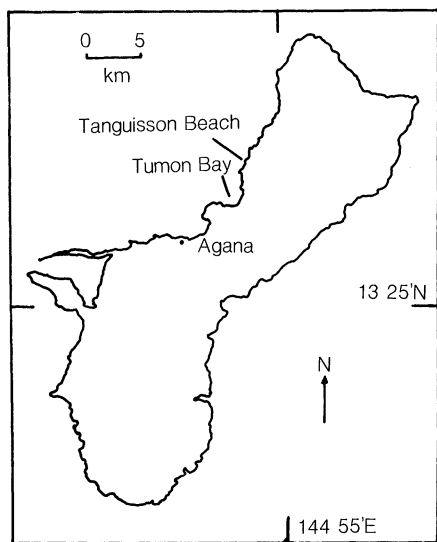


FIG. 1. Location of study sites on Guam, Mariana Islands.

The *Acanthaster planci* outbreaks brought attention to reefs and their disturbances (Connell 1978), which led to questions about the validity of the stability model as an explanation for the species diversity and community structure of coral reef ecosystems.

In a broad sense, disturbances are biological or physical processes that provide space. In sessile communities, disturbances renew this potentially limiting resource and prevent one or a few species from monopolizing an area. In addition to *A. planci* predation, there are numerous disturbances, large and small, that routinely affect coral communities, for example, low tides (Glynn 1976, Loya 1976), violent tropical storms (Glynn et al. 1964, Perkins and Enos 1968, Stoddart 1974, Randall and Eldredge 1977), earthquakes (Stoddart 1972), slumping (Goreau and Goreau 1973), lava flows (Grigg and Maragos 1974), chilling (Shinn 1976), El Niño warmings (Glynn 1983a), bioerosion (Connell 1973, Pang 1973, Scoffin and Garrett 1974, Highsmith 1981), suffocation by blue-green algae (Randall 1973a), and overgrowth by sponges (Bryan 1973) and tunicates (Birkeland et al. 1981). Also, many species prey on reef-building corals causing additional disturbances to the sessile community, e.g., the sea star *Culcita novaeguineae* (Goreau et al. 1972, Glynn and Krupp 1986), the urchins *Diadema* (Bak and Engel 1979) and *Eucidaris* (Glynn et al. 1979), fishes (Randall 1974), and molluscs (Glynn et al. 1972). The variety and frequency of these disturbances lead to a more unpredictable and less stable environment than was conceived previously. Because disturbances are frequent, ecologic climax may be reached only locally, and most coral communities may be maintained in a state of nonequilibrium. In this context, the attack by *Acanthaster planci* is less threatening to the reef community since the coral reef should quickly recover

from the disturbance without any long-term adverse consequences.

Tanguisson Reef on the island of Guam is an ideal setting to examine the recovery of a coral reef. In the summer of 1968, a large population of *Acanthaster planci* (crown-of-thorns) invaded Tanguisson Reef (Fig. 1). By April of 1969 they had disappeared, leaving species richness, coral density, and cover sharply reduced (Randall 1973a). In two of the reef zones, <1% live-coral cover remained after predation by *Acanthaster*. The devastation left in the wake of the crown-of-thorns invasions presented an opportunity to study not only the rate of recovery, but also how reefs recover. In addition to data from this study (1980–1981), data from previous studies in 1970 (Randall 1973a), 1971 (Randall 1973b), and 1974 (Jones et al. 1976) were reanalyzed to give a long-term perspective of recovery. I present here a long-term analysis of the development of a coral community after a catastrophic disturbance.

STUDY SITE

In 1968–1969, Tanguisson Reef on the island of Guam was the site of a major biologic disturbance when the corallivorous starfish *Acanthaster planci* swarmed over the reef community. Many reefs on Guam suffered a similar fate (Chesher 1969a, b), but I selected Tanguisson Reef as the study site in 1980–1981 because for the years 1970, 1971, and 1974, Richard Randall had documented the early stages of coral community recovery at that reef in Randall (1973a, b) and Jones et al. (1976), respectively. His extensive information, both published and unpublished, made Tanguisson Reef an ideal location for a long-term examination of the development of a coral reef community.

Tanguisson Reef is located on Guam's northwestern coast (Fig. 1), and it has five physiographic zones (Fig. 2). Three of these five zones are of particular interest (i.e., reef front, submarine terrace, and seaward slope) because, in those zones, *Acanthaster planci* caused the greatest disturbance. The reef front lies between 1 and 6 m deep and is 50–70 m wide with a series of buttresses and channels that gives this zone a high and variable relief. A decline in the reef-front slope and the absence of the buttress and channel system marks the start of the submarine terrace. The submarine terrace slopes downward from 6 m to a depth of 16 m over a distance from 40 to 110 m, and, in general, its surface relief is less than in adjacent zones. An abrupt increase in slope delineates the beginning of the seaward slope that dips downward from 16 to 33 m over an average distance of 60 m. The overall topographic relief is similar to that of the reef front with many small channels, but the seaward slope's surface is more irregular.

METHODS

Over a 12-yr period, Randall (1970, 1971, and 1974) and I (1980–1981) counted 9693 coral colonies at the

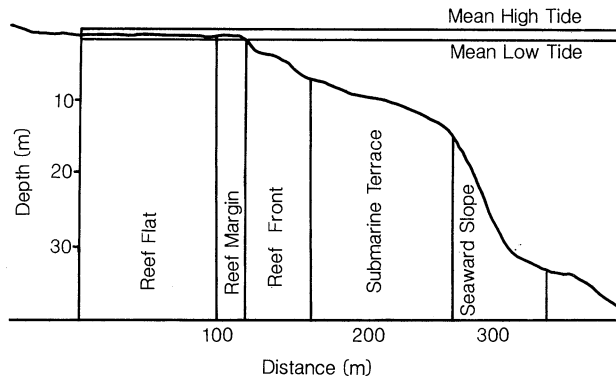


FIG. 2. Reef profile of Transect B at Tanguisson Reef. Vertical exaggeration $\times 5$ (modified after Randall 1973b).

Tanguisson site. These data can be divided into two general categories of information, colony size and colony number. Randall and I used the same method (i.e., transect and 1-m² quadrats) to gather information about the numbers of colonies. But we differed in our methods of collecting size data. In 1980, I used a plotless method (point-quarter: Cottam et al. 1953), in lieu of the quadrats, as a time-saving measure after the results from the two methods were shown not to be significantly different when collecting size data (Colgan 1982).

For this study, the majority of the data presented were collected with 1-m² quadrats. Starting with Randall in 1970 (Randall 1973a), all surveys used the same three transect lines perpendicular to the shore, extending to a depth of 33 m. At 10-m intervals two replicate 1-m² quadrats were used to sample the community. For each coral colony, Randall took two linear measurements and converted them to area estimates by the

formula $A = \left(\frac{\sqrt{1 \cdot x \cdot w}}{2} \right)^2 \pi$. In the 1981 quadrat survey,

I distinguished between adult (longest diameter ≥ 5 cm) and juvenile (longest diameter ≤ 4 cm) coral colonies. This designation did not refer to the coral's reproductive viability, but was used as a means of classifying colonies. Juvenile corals were defined by size alone (longest diameter ≤ 4 cm) following the example in Bak and Engel (1979) who assumed that it takes about a year for most corals to reach that size. Since the 1970 survey began over a year after the swarm of *Acanthaster planci* left the area, it was assumed that most colonies classified as juvenile were recent recruits. Certainly by the 1971 survey, juveniles and recruits were almost synonymous. This distinction based on size excluded species that are commonly found at sizes < 4 cm (e.g., *Stylocoeniella armata*). Also, it is recognized that this designation of juvenile coral overestimates recruits because partial mortality of larger colonies can form small peripheral patches that resemble recruits (Hughes and Jackson 1980). The data collected with quadrats were used in recruitment, density, diversity, distribution, and species-frequency calculations.

In 1980, I used the point-quarter technique (Cottam et al. 1953) to collect size data by placing sampling stations at 2-m intervals along Randall's transect to a depth of 33 m. The area of each coral was calculated using the same formula as used in Randall's studies. From these data, the following were calculated: percent cover, size class distribution, and importance value (Colgan 1981). Importance value was defined as relative percent cover + relative density + relative frequency.

Randall's raw data from the 1970, 1971, and 1974 surveys were reanalyzed, allowing new information to be presented here about the distribution of juvenile and adult corals, species diversity, population density, and recruitment patterns from earlier surveys. With the help of Richard Randall, the species listed in the previous studies have been revised, and are consistent with current nomenclature. Consequently, several species have been synonymized, reducing the species-richness values previously reported.

Species diversity indices were calculated for each zone using the log₂ form (Pielou 1975) of the Shannon-Wiener equation, with p_i = number of colonies: $H' = -\sum p_i \log_2 p_i$; space occupied by species other than living corals was not included as a category for the index (e.g., Grigg and Maragos 1974, Glynn 1976, Loya 1976).

In 1974 at each station, the raw data from the two replicate quadrats were pooled. Unfortunately, this forced replicates from other years to be lumped into one sample for each station, causing all density values to be expressed as colonies per two square metres. In addition, some 1970 raw data were lost, reducing sample sizes for that year as noted on many tables. These reduced samples were used to generate descriptive statistics for zones but were not subjected to parametric analysis.

RESULTS

Species composition

Acanthaster planci prefers to feed on corals of certain species. On Guam, species in the genera *Montipora* and *Acropora* were significantly preferred over all other

TABLE 1. Fifteen most abundant coral species in each of three zones for 1970 and 1981, presented as the percent of the total number of individual colonies sampled. The zones are designated as follows: RF = reef front, ST = submarine terrace, and SS = seaward slope.

RF			ST		SS	
Species	%		Species	%	Species	%
1970						
1 <i>Galaxea fascicularis</i>	15.21		<i>Pavona varians</i>	12.19	<i>Leptastrea transversa</i>	15.92
2 <i>Goniastrea retiformis</i>	10.92		<i>Favia stelligera</i>	6.25	<i>Porites lutea</i>	11.39
3 <i>Favia stelligera</i>	6.17		<i>Galaxea fascicularis</i>	5.94	<i>Leptastrea purpurea</i>	8.23
4 <i>Leptoria phrygia</i>	5.69		<i>Favia pallida</i>	5.63	<i>Porites (S.) rus</i>	7.39
5 <i>Montipora verrilli</i>	5.22		<i>Porites lutea</i>	5.31	<i>Favia pallida</i>	7.59
6 <i>Pocillopora setchelli</i>	5.06		<i>Leptastrea transversa</i>	5.00	<i>Montipora verrilli</i>	7.59
7 <i>Acanthastrea echinata</i>	3.80		<i>Leptoria phrygia</i>	4.38	<i>Stylocoeniella armata</i>	6.33
8 <i>Acropora variabilis</i>	3.64		<i>Pocillopora verrucosa</i>	3.75	<i>Galaxea fascicularis</i>	5.70
9 <i>Porites lutea</i>	3.00		<i>Goniastrea edwardsi</i>	3.44	<i>Montipora caliculata</i>	4.43
10 <i>Favia pallida</i>	2.85		<i>Millipora tuberosa</i>	3.13	<i>Favites russelli</i>	3.16
11 <i>Pocillopora elegans</i>	2.37		<i>Montipora ehrenbergii</i>	3.13	<i>Psammocora</i> sp. 1	3.16
12 <i>Pavona varians</i>	2.06		<i>Montipora verrilli</i>	3.13	<i>Lobophyllia corymbosa</i>	2.52
13 <i>Psammocora nierstraszi</i>	1.58		<i>Porites lobata</i>	3.13	<i>Cycloseris hexagonalis</i>	1.90
14 <i>Montastrea curta</i>	1.58		<i>Acanthastrea echinata</i>	2.81	<i>Acropora humilis</i>	1.90
15 <i>Pavona clavus</i>	1.58		<i>Pavona clavus</i>	2.50	<i>Pavona</i> sp. 1	1.90
			<i>Goniastrea retiformis</i>	2.50	<i>Leptoseris incrustans</i>	1.90
			<i>Goniastrea pectinata</i>	2.50	<i>Echinopora lamellosa</i>	1.90
Species observed	63			44		30
Species sampled	60			41		26
Number of colonies	632			320		159
Area sampled (m ²)	38			40		40
1981						
1 <i>Acropora surculosa</i>	14.79		<i>Leptastrea transversa</i>	16.96	<i>Leptastrea transversa</i>	13.20
2 <i>Galaxea fascicularis</i>	13.48		<i>Montipora elschneri</i>	7.50	<i>Porites lutea</i>	9.52
3 <i>Pocillopora setchelli</i>	10.23		<i>Montipora verrilli</i>	6.84	<i>Porites lobata</i>	6.35
4 <i>Goniastrea retiformis</i>	6.08		<i>Montipora hoffmeisteri</i>	6.28	<i>Favia fava</i>	6.28
5 <i>Montipora elschneri</i>	5.17		<i>Porites lobata</i>	4.98	<i>Astreopora myriophthalma</i>	4.76
6 <i>Favia stelligera</i>	4.96		<i>Porites lutea</i>	3.60	<i>Favia pallida</i>	4.00
7 <i>Leptoria phrygia</i>	3.14		<i>Astreopora myriophthalma</i>	2.83	<i>Montipora foveolata</i>	3.24
8 <i>Acropora nausta</i>	2.84		<i>Favia pallida</i>	2.76	<i>Cyphastrea microphthalma</i>	3.11
9 <i>Montipora verrilli</i>	2.74		<i>Montipora foveolata</i>	2.68	<i>Goniastrea edwardsi</i>	2.79
10 <i>Acropora variabilis</i>	2.74		<i>Millipora tuberosa</i>	2.60	<i>Acropora humilis</i>	2.66
11 <i>Stylophora mordax</i>	2.63		<i>Pocillopora elegans</i>	2.60	<i>Montipora verrucosa</i>	2.47
12 <i>Acropora wardi</i>	1.93		<i>Montipora verrucosa</i>	2.37	<i>Montipora hoffmeisteri</i>	2.28
13 <i>Favia matthaii</i>	1.72		<i>Psammocora</i> sp. 1	1.99	<i>Astreopora gracilis</i>	2.28
14 <i>Acropora cerealis</i>	1.52		<i>Pavona</i> sp. 1	1.98	<i>Favites russelli</i>	2.16
15 <i>Montastrea curta</i>	1.26		<i>Stylophora mordax</i>	1.91	<i>Leptastrea purpurea</i>	1.78
<i>Montipora ehrenbergii</i>	1.26					
Species observed	88			99		107
Species sampled	66			73		73
Number of colonies	987			1306		1576
Area sampled (m ²)	40			42		36

corals (P. W. Glynn and M. W. Colgan, *personal observations*). Following the 1968–1969 outbreak of *Acanthaster*, preferred species were drastically reduced in number and nonpreferred species (e.g., *Porites* spp., *Pocillopora* spp., *Leptastrea* spp., *Favia* spp., and *Goniastrea* spp.) were most common (Table 1). In a short time, preferred species re-established themselves and changed the species composition of the reef (Table 1). The preferred species grew faster and recruited in greater numbers than the nonpreferred species, causing their importance values to rise rapidly, and by 1980, preferred species were predominant on two zones, the reef front and submarine terrace (Table 2). Thus from 1970 to 1980, the species composition of each zone had

TABLE 2. Coral community indices (CCI) are used as an indicator of the change in the species composition with time. CCI = Σ (importance value \times *Acanthaster* prey preference rating).*

Reef zone	1971	1974	1980
Reef front	-32.09	-46.90	+43.71
Submarine terrace	-70.03	-39.97	+73.37
Seaward slope	-173.42	-107.51	-74.97

* *Acanthaster* prey preference rating: +1 for preferred species (e.g., *Montipora* and *Acropora*), -1 for nonpreferred (e.g., *Porites*, *Pocillopora*, *Leptastrea*, *Favia*, and others), and 0 for neutral prey (e.g., *Pavona* and *Astreopora*). An importance value Σ (relative frequency + relative density + relative percent cover) is calculated for each species. The index values range from -300 (all nonpreferred species) to +300 (all preferred species).

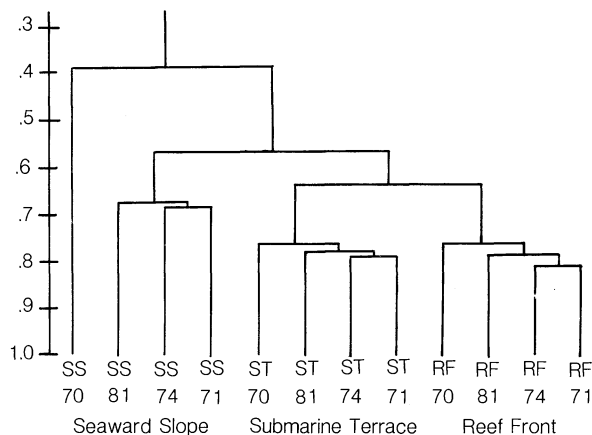


FIG. 3. Dendrogram of the similarity of coral species found in different zones and years. Constructed from the Jaccard similarity indices.

changed from a predominance of nonpreferred prey toward preferred prey of *Acanthaster planci*.

Zonation

In previous studies at Tanguisson Reef, it was assumed that the biological zones were synonymous with the physiographical zones (Randall 1973a, b, Jones et al. 1976, Colgan 1982). A Jaccard similarity coefficients matrix (Sokal and Sneath 1963) of the species present within zones and years validated that assumption. It revealed that the species compositions were more similar within physiographic zones than between zones, regardless of years. A dendrogram constructed from the similarity indices illustrates three distinct clusters (reef front, submarine terrace, and seaward slope) with only the 1970 seaward slope data falling outside the major clusters (Fig. 3).

If recruitment were random, there should be many interzone similarities, because recruits would be distributed evenly across all zones, giving each zone a similar species assemblage. The probability that the species composition of different zones belongs to the same species pool was analyzed with a hypergeometric

TABLE 4. The percent of species ($N \geq 9$ colonies) found predominately in one zone for 1970, 1971, 1974, and 1981. For each of these coral species, a distribution index (χ^2 value) was calculated to determine if a species was randomly distributed over the three zones. The expected values assumed a random distribution and were adjusted for the unequal sampling in each zone. The occurrence of a species in a zone was considered to be other than random if $\chi^2 > 15.507$.

Years	Percent of species found predominately in one zone	Number of species
1970	37.9	29
1971	51.3	37
1974	54.8	42
1981	78.0	45

distribution (methods in Kropp and Birkeland 1982). For the four survey periods, with the exception of the 1970 seaward slope community, there were no significant differences found within zones, only between zones (Table 3). Therefore, either nonrandom recruitment or random recruitment and differential survival caused the species zonation.

Furthermore, a species' tendency to be found in significantly greater numbers in specific zones was tested with 45 species ($n \geq 9$). In 1970, 37.9% of 29 species were associated with a certain zone, and with time, this percentage increased as more corals colonized the reef (Table 4). By 1981, 78.0% of 45 species were associated with a particular zone.

Juvenile corals and recruitment

Juvenile corals were defined by size alone (longest diameter ≤ 4 cm), and their distribution and abundance were examined from data collected from 177 2-m² quadrats and included a sample of 4091 colonies.

From 1970, the juvenile coral density changed significantly in all three zones, reaching a peak in 1974 (reef front, 7.75 colonies/m²; submarine terrace, 12.30/m²; and seaward slope, 12.70/m²; Table 5). These mean densities were lower than those recorded in either Caribbean reefs (17/m²; Bak and Engel 1979) or the Great

TABLE 3. The probability that coral species from different zones and years are members of the same species pool. The probabilities were calculated using the hypergeometric distribution. * $P < .05$, ** $P < .01$, *** $P < .001$. RF = reef front, ST = submarine terrace, SS = seaward slope.

RF 70	...											
ST 70	***	...										
SS 70	***	***	...									
RF 71	.278		***	...								
ST 71	***	.188	**	**	...							
SS 71	***	**	*	***	*	...						
RF 74	.337	***	***	.547	**	***	...					
ST 74	***	.55	**	**	1.00	*	**	...				
SS 74	***	**	**	***	**	.367	***	**	...			
RF 81	.708	*	***	.488	*	***	1.00	*	***	...		
ST 81	**	.44	***	**	.62	*	***	.79	**	**	...	
SS 81	***	***	**	***	***	.151	***	***	.251	***	***	...
RF 70		ST 70	SS 70	RF 71	ST 71	SS 71	RF 74	ST 74	SS 74	RF 81	ST 81	SS 81

TABLE 5. Density of juvenile (diameter ≤ 4 cm) coral colonies, calculated for zones and years. Data are means with 95% CI (N = number of 2-m² quadrats). A two-way ANOVA with 18 replicates was used to analyze the data for 1971, 1974, and 1981. A random number table was used to discard replicates in excess of 18 for the two-way ANOVA. *** $P < .001$.

Reef zone	1970	1971	1974	1981
	No./2 m ² (N)	No./2 m ² (N)	No./2 m ² (N)	No./2 m ² (N)
Reef front	10.7 \pm 4.05 (16)	13.5 \pm 4.94 (19)	15.5 \pm 7.63 (19)	16.4 \pm 1.52 (20)
Submarine terrace	15.8 \pm 3.33 (7)	19.8 \pm 3.68 (20)	24.6 \pm 4.48 (21)	10.7 \pm 2.72 (21)
Seaward slope	9.0 \pm 4.74 (8)	18.6 \pm 2.87 (20)	25.4 \pm 4.67 (19)	24.3 \pm 3.51 (18)
Source of variation				
		df	MS	
Subgroups		8	842.77	
Years		2	593.38***	
Zones		2	1947.27***	
Interaction (years \times zones)		4	415.22***	
Within subgroups		153	70.85	
Total		161		

Barrier Reef (15/m²; Connell 1973). After 1974, there was a significant decline in the densities of juveniles in two zones (reef front: $t_{37} = 2.35$, $P < .05$; submarine terrace: $t_{40} = 5.21$, $P < .001$). Although juvenile coral density reached its highest level in 1974, it was in 1970 and 1971 that the greatest proportion of the coral population was made up of juveniles (Table 6A).

Juvenile corals found within a 2-m² quadrat without conspecific adults are defined as independent juveniles. These juvenile corals are pioneers, settling in areas where their adults are not found in close proximity. In the wake of the predation of the crown-of-thorns, few adult-sized corals remained, and those that remained were scattered. The reestablishment of the coral community was the result of the initial settlement of independent juvenile corals. In 1970, in two zones (submarine terrace and seaward slope) where *Acanthaster* predation had devastated coral populations, independent juveniles contributed $> 75\%$ of the juvenile coral population (Table 6B). Subsequently, the percentage of independent juveniles declined in all zones.

To test if juvenile corals were found preferentially in specific zones, the distribution of 28 species with > 16 juveniles censused in any one year were examined with a chi-square goodness-of-fit test. From 1971, 1974,

and 1981, 50 distribution patterns were examined and 46 showed a significant preference for a specific zone (Table 7). In 1981, of the 18 species examined, only two species (i.e., *Acropora humilis* and *Stylophora mordax*) were not associated with a specific zone.

Juveniles not only showed zone-specific recruitment and survival, but, by 1974, they were found in the greatest numbers in the same zones where their adults were most abundant. In 1971, 39% of the 23 species examined had both the adults' and juveniles' highest abundances in the same zones, and by 1981, this value rose to 87%, which was a significant change (Cochran's $Q = 13.9$, $P < .001$).

Once adults were established, the likelihood of juveniles settling and surviving in their vicinity increased. This is seen in a significant positive relationship between the abundance of adults and juvenile conspecifics. As early as 1970, two zones (reef front and submarine terrace) showed significant positive correlations between the abundances of adult and juvenile conspecifics (Table 8), and, by 1971, all zones showed a similar relationship ($P < .001$).

It has been suggested that juveniles disperse away from conspecifics instead of to them (Connell 1973). A coefficient of association (Krebs 1972:383) between

TABLE 6. Relative abundance of juvenile (diameter ≤ 4 cm) corals in three zones of Tanguisson Reef in four years.

A) Percent of corals that were juveniles in N 2-m ² samples.				
Reef zone	1970	1971	1974	1981
	% (N)	% (N)	% (N)	% (N)
Reef front	36.55 (632)	32.53 (789)	32.09 (919)	12.96 (987)
Submarine terrace	67.56 (320)	62.66 (632)	49.90 (1035)	17.20 (1306)
Seaward slope	88.88 (159)	73.10 (521)	59.07 (817)	27.74 (1576)
B) The percentages of juvenile coral colonies that were independent (i.e., without a conspecific adult within a 2-m ² quadrat) in a sample of juveniles.				
Reef zone	1970	1971	1974	1981
Reef front	36.26	28.89	22.58	6.06
Submarine terrace	76.11	53.83	34.47	20.74
Seaward slope	100.00	55.81	42.52	12.35

TABLE 7. The number of coral species ($N \geq 16$ colonies) whose juveniles (diameter ≤ 4 cm) exhibited a significant preference in their distribution for a certain zone in 1971, 1974, and 1981. A chi-square goodness-of-fit test was used to determine whether the juvenile coral distribution was random among zones. The expected values assumed a random settlement and were adjusted for unequal sampling in each zone.

Year	Number of species whose juveniles exhibited preference for a specific zone	Number of species with a random distribution
1971	12	1
1974	18	1
1981	16	2

adults and juveniles in the same 2-m² quadrat tested that observation for 34 species. In 1971, 50% of the species showed significant positive associations between adult and juvenile (Table 9). With time, adult-juvenile associations increased (Friedman's test, $X^2_2 = 31.824$; $P < .001$, rising to 79% by 1981).

Such positive associations would tend to produce clumped instead of either random or even coral distributions. From 354 quadrats for the years 1971, 1974, and 1981, an examination of 150 dispersion patterns of 44 species within zones showed clumped distributions in 87.3% of the case (coefficient of dispersion, $S^2/\bar{Y} > 1.50$, $n \leq 10$ colonies per zone). Of the 19 cases of random distribution, 89.5% were from the suborder Astrocoeniina of which 33.3% were members of the family Pocilloporidae.

Diversity

It is expected that *Acanthaster planci* predation would reduce coral cover and density, but the starfish also lowered species richness and diversity. After *A. planci* left Tanguisson Reef, only 84 species were found, a reduction of 47 species (Randall 1973c). The number of species did not stay depressed for long. With the growth of small coral patches that survived the outbreak of *A. planci* and the recruitment of new species from neighboring areas, species richness rose quickly

(Table 1). By 1974, 115 species were found on Tanguisson Reef, and in 1981, 154 species were identified there (Colgan 1981).

This rise in species richness was apparent at two sampling levels: throughout the reef (as mentioned above) and within quadrats. In 1970, the reef front had a mean of 5.4 species/m² within a quadrat, the submarine terrace had 4.9 species/m², and the seaward slope had 2.0 species/m². In the years to follow, there were significant increases in the species richness per quadrat (Table 10), the result of the recruitment of independent juvenile corals (e.g., 1981 seaward slope, 26.3 species/m²).

Since diversity indices are often used to measure the health of communities, I was interested to see if they could gauge the condition of the reef and indirectly the level of the disturbance. In 1970, the total diversity of the zones was high (reef front, 4.87; submarine terrace, 4.81; and seaward slope, 4.04). This was a surprising result since the predation had reduced species richness and coral cover (<1% coral cover on the submarine terrace and seaward slope). These high diversity values resulted from the presence of numerous small coral recruits and remnants of surviving corals. Throughout the study, the pattern of changing diversity values was different for each of the three zones. From 1970, the diversity of the reef front did not change significantly (Table 11). The diversity of the submarine terrace fluctuated around the value of 4.8, with the only significant change occurring between 1974 and 1981 (0.4025 > MSD [minimum significant difference]; $P < .05$; Games and Howell method: Sokal and Rohlf 1981). In 1970, the seaward slope's coral species diversity was at its lowest, but diversity increased significantly in the following years. In 1981, the seaward slope had the highest diversity value, $H' = 5.096$.

Growth forms

The corals that survived the predation of the crown-of-thorns fell into two categories; corals either were completely bypassed (Done 1985) or were partially eaten. Since corals in the latter category were but small patches, many took on what appeared to be an en-

TABLE 8. Correlation coefficients with 95% confidence limits (L = lower limit, U = upper limit) between adult (diameter ≥ 5 cm) and juvenile (diameter ≤ 4 cm) conspecifics' abundances within zones and years. A test of homogeneity of the correlation coefficients (Sokal and Rohlf 1981) within zones was used for this analysis. NS > .05, * $P \leq .05$, ** $P \leq .01$, *** $P \leq .001$.

Reef zone	1970	1971	1974	1981
Reef front	$r = 0.615^{***}$ (53) L = 0.406 U = 0.762	$r = 0.653^{***}$ (60) L = 0.475 U = 0.786	$r = 0.497^{***}$ (62) L = 0.278 U = 0.667	$r = 0.918^{***}$ (66) L = 0.867 U = 0.950
Submarine terrace	$r = 0.403^*$ (35) L = 0.066 U = 0.657	$r = 0.746^{***}$ (50) L = 0.604 U = 0.843	$r = 0.921^{***}$ (63) L = 0.879 U = 0.952	$r = 0.950^{***}$ (74) L = 0.920 U = 0.969
Seaward slope	$r = -0.189$ NS (20) L = -0.603 U = 0.305	$r = 0.532^{***}$ (57) L = 0.322 U = 0.682	$r = 0.913^{***}$ (60) L = 0.857 U = 0.948	$r = 0.862^{***}$ (73) L = 0.786 U = 0.912
Reef front	$\chi^2 = 47.740^{***}$			
Submarine terrace	$\chi^2 = 55.589^{***}$			
Seaward slope	$\chi^2 = 55.190^{***}$			

TABLE 9. Association coefficient (V) between juvenile corals (diameter ≤ 4 cm) and adult corals (diameter ≥ 5 cm) calculated for 34 species for 1971, 1974, and 1981. The coefficient ranges from -1 to $+1$ with 0 indicating independence. A 2×2 contingency test was used to determine the probability of an association [$p(\chi^2)$].† A dash indicates an absence of either adults or juveniles in the sample.

Species groups	Years (blocks)					
	1971		1974		1981	
	V	$p(\chi^2)$	V	$p(\chi^2)$	V	$p(\chi^2)$
<i>Psammocora nierstraszi</i>	0.502	**	0.244	NS	0.680	***
<i>Psammocora</i> sp. 1	-0.070	NS	-0.035	NS	0.534	***
<i>Stylophora mordax</i>	—	—	0.195	NS	0.026	NS
<i>Pocillopora elegans</i>	0.628	***	0.250	NS	0.411	**
<i>Pocillopora setchelli</i>	0.413	**	0.557	***	0.740	***
<i>Pocillopora verrucosa</i>	0.134	NS	0.556	**	0.644	***
<i>Acropora humilis</i>	-0.062	NS	0.151	NS	0.224	NS
<i>Acropora nasuta</i>	0.332	NS	0.101	NS	0.483	**
<i>Acropora surculosa</i>	0.442	**	-0.099	NS	0.540	***
<i>Astreopora myriophthalma</i>	0.153	NS	0.329	*	0.508	***
<i>Montipora elschneri</i>	0.300	NS	0.101	NS	0.435	**
<i>Montipora foveolata</i>	—	—	0.131	NS	0.455	**
<i>Montipora hoffmeisteri</i>	-0.053	NS	0.151	NS	0.505	***
<i>Montipora verrilli</i>	0.440	**	0.267	NS	0.456	**
<i>Montipora verrucosa</i>	-0.051	NS	-0.056	NS	0.282	NS
<i>Pavona</i> spp.‡	0.687	***	0.319	NS	0.575	***
<i>Porites lichen</i>	0.116	NS	0.319	NS	0.318	NS
<i>Porites lobata</i>	0.427	**	0.489	***	0.785	***
<i>Porites lutea</i>	0.165	NS	0.323	*	0.500	***
<i>Porites</i> (S.) <i>rus</i>	0.371	**	0.438	**	0.349	*
<i>Favia favius</i>	0.165	NS	0.323	*	0.599	***
<i>Favia pallida</i>	0.094	NS	-0.001	NS	0.465	***
<i>Favia stelligera</i>	0.461	**	0.437	**	0.294	NS
<i>Favites russelli</i>	0.260	*	0.811	***	0.581	***
<i>Goniastrea edwardsi</i>	0.348	**	0.343	*	0.531	***
<i>Goniastrea pectinata</i>	0.448	**	0.090	NS	0.521	***
<i>Goniastrea retiformis</i>	0.6645	***	0.681	***	0.497	***
<i>Platygyra pini</i>	0.276	NS	0.106	NS	0.359	NS
<i>Leptoria phrygia</i>	0.276	NS	0.165	NS	0.391	*
<i>Leptastrea purpurea</i>	0.589	***	0.484	**	0.291	NS
<i>Leptastrea transversa</i>	0.518	***	0.668	***	0.658	***
<i>Cyphastrea</i> spp.§	0.245	NS	0.257	NS	0.644	***
<i>Galaxea fascicularis</i>	0.371	**	0.438	**	0.689	***
<i>Millepora tuberosa</i>	0.348	*	0.539	***	0.384	**
Friedman's analysis ranks ΣR_{ij}	55		60		89	

$$\chi^2 = \frac{12(55^2 + 60^2 + 89^2)}{3(34)(3 + 1)} - 3(34)(3 + 1)$$

$$= 31.824^{***}$$

† NS > .05, * $P \leq .05$, ** $P \leq .01$, *** $P \leq .001$. Friedman's method for randomized blocks (Sokal and Rohlf 1981:446) was used to determine if there was a significant change in the coefficient of association with time.

‡ *Pavona varians* and *Pavona* sp. 1 were combined.

§ *Cyphastrea chalcidicum*, *Cyphastrea microphthalma*, and *Cyphastrea serailia* were combined.

TABLE 10. The number of species calculated for zones and years. Data are means with 95% CI (N = number of 2-m² quadrats). A two-way ANOVA with 18 replicates was used to analyze the data for 1971, 1974, and 1981. A random number table was used to discard replicates in excess of 18 for the two-way ANOVA. *** $P < .001$.

Reef zone	1970	1971	1974	1981
	No./2 m ² (N)	No./2 m ² (N)	No./2 m ² (N)	No./2 m ² (N)
Reef front	10.8 \pm 2.01 (6)	13.3 \pm 2.34 (19)	15.0 \pm 2.547 (19)	14.9 \pm 2.49 (20)
Submarine terrace	9.7 \pm 1.75 (7)	12.7 \pm 1.67 (20)	17.9 \pm 1.56 (21)	21.7 \pm 2.18 (21)
Seaward slope	4.1 \pm 1.89 (8)	12.1 \pm 1.74 (20)	16.0 \pm 1.74 (19)	26.3 \pm 1.97 (18)
Source of variation	df		MS	
Subgroups	8		387.79	
Years	2		949.45***	
Zones	2		181.52***	
Interaction (years \times zones)	4		210.10***	
Within groups	153		20.69	
Total	161			

TABLE 11. Total Shannon-Wiener species diversity indices ($H' = -\sum p_i \log_2 p_i$) \pm standard error for zones and years, the values corrected for bias. The values and standard errors were calculated according to the methods given in Poole (1974: 392). N = number of colonies.

	1970	1971	1974	1981
	$H' \pm SE (N)$	$H' \pm SE (N)$	$H' \pm SE (N)$	$H' \pm SE (N)$
Reef front	4.8708 \pm 0.071 (632)	4.7174 \pm 0.0684 (789)	4.7149 \pm 0.0598 (919)	4.7080 \pm 0.0604 (987)
Submarine terrace	4.8111 \pm 0.0769 (320)	4.8190 \pm 0.0693 (632)	4.5943 \pm 0.0637 (1035)	4.9968 \pm 0.0455 (1306)
Seaward slope	4.0401 \pm 0.112 (159)	4.7905 \pm 0.0961 (521)	4.5467 \pm 0.0671 (817)	5.0957 \pm 0.043 (1576)

crusting form. For example, if after predation on a corymbose colony only a small piece of the base survived either exposed on the surface or tucked into some irregular cranny of the reef, it would be classified as an encruster, as would the newly settled recruits, which initially take on an encrusting growth form. In 1970, these early encrusters accounted for 68% of the corals, and by 1971 their numbers increased to 74% (Colgan 1981). This rise coincided with increased coral recruitment. After 1971, encrusting forms declined because recruits with ephemeral encrusting growth forms and remnant patches of surviving corals had developed into other growth forms (i.e., massive, corymbose, and so on). In all reef zones, many of the early two-dimensional colonies developed into three-dimensional growth forms, increasing the reef's topographic complexity. However, the submarine terrace did not increase in surface heterogeneity and complexity as dramatically as did the other zones because of the abundance of perpetual encrusters such as *Montipora* spp. and *Leptastrea* spp.

Size distribution, coral coverage, and density

In 1970, most coral colonies were either newly settled recruits or remnants of much larger colonies; this condition skewed the size class distributions toward smaller corals (Colgan 1981). The crown-of-thorns'

devastation of the seaward slope and submarine terrace left a predominance of small-sized corals (99% of the colonies were <10 cm in diameter and 83% <5 cm diameter; Table 12). The reef front, least affected by *A. planici*, had the largest colonies and the least skewed distribution. By 1980, with growth of recruits and patches that survived the predation, colony size increased, and as the reef recovered, the size class distribution became more even (Table 12).

Percent live coral is frequently used as a measure of the health of the reef and as a means of measuring recovery after a disturbance. Since there were no studies of the condition of Tanguisson Reef before the invasion of the starfish, I had to rely on data from the nearby reef in Tumon Bay (Randall 1973c). At Tumon Bay, the coral cover was as follows: reef front, 49%; submarine terrace, 59%; seaward slope, 50%. In 1970 at Tanguisson Reef, 1 yr after the predation by *A. planici*, the surface coverage was 21, 0.9, and 0.5%, respectively (Table 13). In 1980, all zones had significantly increased their coral coverage: reef front, 43%; submarine terrace, 66%; seaward slope, 36%. Two possible causes for increased cover were the growth of colonies and the increased density of colonies. For 1970, 1971, 1974, and 1981, the average coral size and density were correlated with percent cover within zones using Spearman's correlation. There was a positive correlation be-

TABLE 12. Distribution of corals by size class (diameter in centimetres) from 1970 to 1980. Data from all transects within a zone are combined and expressed in relative values, with size class evenness value ($J' = -\sum p_i \log_2 p_i / \log_2 n$). Point-quarter technique used to collect 1980 data.

Size class (cm)	Reef front				Submarine terrace				Seaward slope			
	1970	1971	1974	1980	1970	1971	1974	1980	1970	1971	1974	1980
0-5	49.68	41.32	41.94	15.93	85.94	71.36	61.84	16.41	83.85	82.15	69.65	32.60
6-10	31.65	40.18	38.78	25.82	13.44	23.10	26.09	22.66	15.53	14.78	23.62	33.42
11-15	9.34	9.76	9.15	21.98	0.63	4.59	6.76	17.18	0	2.69	4.41	17.12
16-20	2.85	3.80	4.58	11.26	0	0.47	2.80	15.63	0.62	0.19	2.08	7.07
21-25	2.06	1.65	2.18	6.87	0	0.32	1.55	8.01	0	0.19	0	4.35
26-30	1.74	1.77	1.53	4.94	0	0.16	0.68	5.66	0	0	0.12	3.30
31-35	0.32	0.51	0.76	4.40	0	0	0.19	6.84	0	0	0.12	1.36
36-40	0.95	0.13	0.22	1.92	0	0	0	1.76	0	0	0	0.82
41-45	0.79	0.38	0.33	2.50	0	0	0	2.73	0	0	0	0
46+	0.63	0.51	0.54	4.39	0	0	0.10	2.73	0	0	0	0
Number of colonies	632	789	918	364	320	632	1035	512	161	521	817	368
J'	0.57	0.57	0.58	0.87	0.19	0.34	0.45	0.88	0.20	0.25	0.36	0.68

TABLE 13. Percent live coral cover for zones and years. Two Friedman's randomized block tests (Sokal and Rohlf 1981: 446) were used to analyze for differences among years and among zones.

Reef zone	1970	1971	1974	1981	R
Reef front	20.9	21.9	24.8	43.7	11
Submarine terrace	0.9	4.0	12.0	65.9	9
Seaward slope	0.5	2.1	6.3	36.2	4
ΣR_{ij}	3	6	9	12	
Years: $X^2 = \frac{12(3^2 + 6^2 + 9^2 + 12^2)}{4(3)(4 + 1)} - 3(4)(4 + 1) = 9^*$					
Zones: $X^2 = \frac{12(4^2 + 9^2 + 11^2)}{4(3)(3 + 1)} - 3(4)(3 + 1) = 6.5^*$					

* $P < .05$ (significance of differences among years or zones).

tween increasing colony size and cover ($r_{11} = 0.928$, $P < .001$), whereas no correlation was found between density and cover ($r_{11} = 0.424$, $P > .05$).

All zones increased in coral cover with time, but they did not do so at the same rate. The submarine terrace had the fastest increase in coral cover because of the predominance of fast-growing encrusting corals (e.g., *Montipora* spp.). By 1981, the other two zones, with a prevalence of slower growing species, had not yet reached the values projected for pre-*Acanthaster planci* levels. If those trends had been maintained, by 1984 both zones probably would have reached Tumon Bay levels. However, in 1981, *A. planci* again became common and apparently set back the succession of the reef recovery, although to a lesser extent than in 1968–1969 (Birkeland 1982, Colgan 1982).

Since 1970 in the three reef zones, the density of coral colonies rose significantly as the result of juvenile coral settlement (Table 14). In 1981, the highest density was found on the seaward slope, which had the lowest percent coral cover and the smallest corals.

DISCUSSION

In 1968–1969, the Tanguisson reef coral community experienced a catastrophic disturbance (as defined in

Harper 1977, Paine 1979), when a large swarm of *Acanthaster planci* left few corals alive. Four categories of coral survivors were found after the event.

First, most of the corals living in shallow turbulent waters, <2 m in depth, were not attacked. Because surge and turbulence cause *Acanthaster planci* to lose their hold and be tossed around (Goreau et al. 1972, Birkeland and Randall 1979), they are excluded from heavily wave-assaulted areas (Laxton 1974).

Second, below this refuge, scattered patches of non-preferred corals were bypassed by the crown-of-thorns, like the patches of nonpreferred prey observed in Hawaii (Branham et al. 1971), on the Great Barrier Reef (Endean 1973), on Saipan (Goreau et al. 1972), in the Eastern Pacific (Glynn 1976), and in American Samoa (Birkeland and Randall 1979). The nonpreferred prey fell into two categories: coral species that the crown-of-thorns usually does not eat (e.g., *Millepora*, *Porites*, *P. [Synarea]*) and species that would be eaten (*Pocillopora* and *Stylophora*) if not for the protection of their crustacean symbionts (Glynn 1976, 1980, 1983b). In addition to protecting their hosts, the behavior of these symbionts indirectly protects adjacent colonies, resulting in a halo of uneaten colonies around the defended colony (M. W. Colgan, *personal observation*) or uneaten colonies in a centrally located area refuge (Glynn 1985).

Third, both preferred and nonpreferred prey survived as partially eaten colonies. These remnant patches represented a good sample of the previous community from which to draw on for recruits. Besides contributing to the recruits, these remnant corals grew increasing coral cover (Fishelson 1973, Glynn 1974, Colgan 1982).

The last category of survivors was found in cryptic interstices of the reef where the starfish did not reach. Typical of these corals are the small encrusting corals *Stylocoeniella armata* and *Pavona* sp. that survived in high numbers (e.g., their combined abundance on the 1970 seaward slope was 10.76% compared with 0.69% in 1981).

TABLE 14. Density of coral colonies calculated for zones and years. Data are means with 95% CI (N = number of 2-m² quadrats). A two-way ANOVA with 18 replicates was used to analyze the data. A random number table was used to discard replicates in excess of 18 for the two-way ANOVA. NS = $P > .05$, * $P < .05$, ** $P < .01$, *** $P < .001$.

	1970	1971	1974	1981
	No./2 m ² (N)	No./2 m ² (N)	No./2 m ² (N)	No./2 m ² (N)
Reef front	33.3 ± 5.78 (19)	41.5 ± 9.76 (19)	48.3 ± 15.01 (19)	49.4 ± 9.12 (20)
Submarine terrace	16.0 ± 3.76 (20)	31.6 ± 5.24 (20)	49.3 ± 4.94 (21)	62.2 ± 8.18 (21)
Seaward slope	7.9 ± 2.37 (20)	26.1 ± 3.58 (20)	43.0 ± 3.58 (20)	87.6 ± 6.65 (18)
Source of variation	df		MS	
Subgroups	11		8228.14	
Years	3		22 393.00***	
Zones	2		168.88 NS	
Interaction (years × zones)	6		3832.13***	
Within groups	204		290.00	
Total	215			

The small patches of survivors contributed to the high diversity and species richness values in all zones following predation, but because of their small size, coral cover was still low. In the submarine terrace and seaward slope zones these small patches accounted for <1% of the surface cover. I have no direct proof about the source of the planula, but it seems reasonable that these remnant corals could have provided a local source of recruits as well as providing in situ colonies from which the reef could be repopulated. Because the reef community did not seem to rely strictly on outside sources for colonizers, recovery would be accelerated (Connell and Slatyer 1977).

Space is considered to be an important limiting resource in sessile communities (Connell 1961, 1978, Paine 1966, 1984, Dayton 1971). In the aftermath of the predation by *A. planci*, space was apparently abundant, but recruits did not immediately take advantage of this abundant resource; instead they reached a peak in 1974. In 1970 and 1971, the abundance of planulae and not space seemed to limit the settlement of juvenile corals. Although these results could be explained either by high settlement with high mortality or by the space being occupied (e.g., algal cover prohibiting larval settlement), settling plate data showed that settlement was limited even though space was apparently available (Birkeland et al. 1982). In 1974, after an establishment of large adult coral population, which may have provided more nearby sources for planulae production, the juvenile coral density reached its peak. Thus, the recovery through recruitment can be viewed as a positive feedback system with the establishment of adults enhancing recruitment, which in turn establishes more adults, until, finally, space becomes limiting and the proportion of recruits decreases (Table 6A).

The adult colonies were re-established through regrowth of surviving patches and growth of recruits. In 1970 and 1971, because there were so few adult colonies, most of the corals were "independent" juveniles. These pioneer juveniles established coral colonies away from the immediate vicinity of the few remaining adults and produced a somewhat random dispersion pattern within a zone. With an ever increasing and more dispersed adult population, the importance of these "independent" juveniles declined. By 1981, there were statistically significant associations between the presence of adult and juvenile conspecifics. Eventually, this affinity between juveniles and adults resulted in a contagious settlement pattern (Lewis 1974, Dana 1976), and by 1981, species distributions within a zone had shifted from a random to a clumped pattern.

Many coral species either preferred to settle or survived better in certain zones, and in 1981 adult and juvenile conspecifics were abundant in the same zone. But during the early stages of recovery, adult and juvenile conspecifics were found inhabiting different zones. The crown-of-thorns disproportionately reduced the adult coral populations, statistically shifting

their distributions to favor zones where the corals were not most frequently found. Recruits re-established the species in the zones in which they were most abundant. Thus, the species assemblages resulted from nonrandom recruitment or survival of juveniles. The ultimate cause of a coral's nonrandom distribution may be the planula's response to physical factors such as light, substrate (Yonge 1973), and water motion (Jokiel 1978). Also, selective predation may limit distribution of a few species (Neudecker 1979, Wellington 1982).

Nonrandom recruitment or survival of juveniles along with the strong positive correlation between adult and juvenile abundances produced the distinct species assemblage of each zone. With time, this correlation increased significantly as the species that normally inhabited the zone re-established themselves. By 1981, the positions of the most abundant species were reinforced through disproportionate recruitment (Connell 1973, Grigg and Maragos 1974, Loya 1976). Without additional disturbances, small and large, to reverse this trend, the reef could become increasingly stratified with a few predominate species in each zone. On atolls, where disturbance levels are less than on high islands such as Guam (Birkeland and Randall 1979, Birkeland 1982), zones are highly stratified (Wells 1954). In the absence of major disturbances, this striking zonation developed because few species were able to dominate a zone.

Twelve years after the disturbance, species richness and diversity were still on the increase, and these values have reached or exceeded measurements of comparable reefs before the catastrophe (i.e., Tumon Bay: Randall 1973c). The recovery occurred faster than predicted by the stable equilibrium model of Endean (1973) and Grassle (1973) because long-term successional changes were not required to give the appearance of a mature, diverse community. Recovery was greatly accelerated because *A. planci* did not destroy the structural integrity of the reef framework. This provided a stable platform for regrowth and resettlement, and the surviving complex structure offered a refuge for recruits.

At Tanguisson, the stable equilibrium model cannot adequately explain either the rapid rate of recovery or the present community structure. Thus, other explanations are required. Connell (1978) discussed six hypotheses that could explain the diversity and community structure of a coral reef: (1) niche diversification, (2) circular networks, (3) compensatory mortality, (4) gradual change, (5) equal chance, and (6) intermediate disturbance. At Tanguisson Reef, the hypotheses of intermediate disturbances and compensatory mortality are applicable.

For a coral reef community, compensatory mortality would occur when either predation or disturbance disproportionately affected the species that occupy the most space (Connell et al. 1984). On the island of Guam, *Acanthaster* does have a feeding preference (e.g., *Ac-*

ropora spp. and *Montipora* spp.: P. W. Glynn and M. W. Colgan, *personal observations*), and in 1971, non-preferred species (e.g., *Porites* spp. and *Pocillopora* spp.) were the predominant corals in all zones. Their predominance was short-lived and, by 1980, preferred prey had become more important with regard to frequency, density, and cover (Table 2). Preferred prey quickly recovered because of their higher rate of recruitment and faster growth than the nonpreferred species that had an initial advantage in number and size. The predation of these faster growing preferred species results in compensatory mortality. Without further perturbations, these preferred species of the genera *Acropora* and *Montipora* could come to dominate the reef and thus lower the diversity.

On Guam's reefs, disturbances are commonplace (e.g., Chesher 1969a, Bryan 1973, Randall 1973a, Randall and Eldredge 1977) and as this study shows, a disturbance can shape the reef's community structure. As reported in other marine communities (Paine 1966, Dayton 1971, Levin 1976, Connell 1978, Sousa 1979a, b), predators, like *Acanthaster*, disturb sessile communities, and can help to prevent local competitive elimination of species, producing higher community species diversity (Sousa 1979a). On Guam, disturbances, such as the 1968–1969 outbreak of *Acanthaster planci*, that are intermediate in either their intensity or frequency may maintain the reef's high diversity (Connell 1978).

At Tanguisson Reef, some smaller disturbances include storms (Randall and Eldredge 1977), small *A. planci* outbreaks (Birkeland 1982, Colgan 1982), fish predation (Neudecker 1979), overgrowth by an encrusting sponge (Bryan 1973, Plucer-Rosario 1987) and a blue-green alga (Randall 1973a), among others. The degree to which these perturbations disturb the community varies locally, causing unequal successional setbacks within unique patches (Levin 1976, Paine and Levin 1981). These smaller disturbances were superimposed on the reef while it recovered from the major crown-of-thorns disturbance. This resulted in a mosaic landscape of unsynchronized successional patches (Levin and Paine 1974, Paine and Levin 1981, Sousa 1984), which added to the overall species diversity and heterogeneity of the reef community.

Within a period of 12 yr at Tanguisson Reef, measurements of species diversity, percent cover, growth-form diversity, size class evenness, and species richness approached or exceeded values at a comparable reef area before the outbreak. This rapid recovery from a natural disturbance demonstrates that some coral communities have a greater resilience than was once believed.

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